A BOTANICAL CRITERION OF THE ANTIQUITY OF THE ANGIOSPERMS

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As to the origin of the angiosperms, that group of seed plants which is now such a dominant element in the earth's vegetation, we know almost nothing. They first appear as fossils in the deposits of the lowest Cretaceous in eastern North America, Alaska, Greenland, and Portugal, but just where they actually originated, and how long ago, are still matters of great uncertainty. The aim of the present paper is to throw a little light on the antiquity of this great plant group by studying the rate of evolution displayed by its members.

Evolution has not been a uniformly rapid process. The fact that plants recognized as "primitive" and others recognized as "recent" exist together at the present time makes it evident that certain vegetable types have changed but little throughout long geological periods, whereas others have for one cause or another become altered much faster. The degree of inherent "variability" and the frequency of hybridization have doubtless been influential in determining this rate of change, but a more important factor perhaps than either seems to be the length of the generation or period from seed to seed. A plant in which this cycle is completed in a year or two is able to multiply its generations more rapidly, and thus to accumulate heritable changes much faster, than one which requires a longer time for the attainment of reproductive maturity. This length of generation is definitely correlated with the growth habit of the plant, being greatest in trees—which usually reach an age of from fifteen to twenty years (in many cases much more) before bearing fruit—less in shrubs, and shortest of all in herbs, where one or two seasons from seed suffice to produce a fruiting plant again. In a given length of time, therefore,

a herbaceous species will pass through a much larger number of generations than a woody one, and will consequently tend, other factors being equal, to become changed in type much more rapidly. We should thus expect the herbaceous element in the vegetation to have been evolved at a much faster rate than the woody element. The establishment of this as a fact, taken with what we know as to the history and present numerical status of herbs and woody plants, will provide us with a valuable clue as to the antiquity of the angiosperms.

That herbs are indeed subject to more rapid changes than any other plant type is indicated by the fact that the first local species and genera to develop in a region subsequent to its isolation have apparently almost always been herbs. This is well illustrated by a comparison of the floras of temperate North America and of Europe. On these continents today there are many local or "endemic" genera which are limited in their distribution to one or to the other. Certain of these are evidently "relict" endemics, isolated survivors of types once much more widely disseminated. They may be recognized from the fact that they stand without near relatives in the floras; and many of them, such as sassafras and hickory, occur as fossils on both sides of the Atlantic. These relicts doubtless constitute a very ancient floral element, and it is significant that among them are practically all the genera of trees and shrubs which are local to either North America or Europe. The majority of the endemic genera, however, seem to belong to quite a different category, for they occur in groups of from three to twenty genera, the members in each of which are closely related to one another, each group apparently to be looked upon as a separate center of evolution and the nucleus of a new family. The genera centering around *Lesquerella* in the Cruciferae, around *Eriogonum* in the Polygonaceae, around *Godetia* in the Onagraceae, around *Pentstemon* in the Scrophulariaceae, and around *Solidago* in the Compositae, are a few of the sixty or more such groups in the dicotyledonous flora of North America, and there are as many in Europe. These "indigenous" endemic genera most probably had their origin on their respective continents, since a free interchange of plants between America and Europe was interrupted, presumably

in the Early or Middle Tertiary; for had they existed before that date in anything like their present numbers and importance, it is highly unlikely that they would now be represented in the floras of both hemispheres. During the time since the isolation of the two continents, and while the rest of the flora have remained unchanged or have been developing endemic species merely, these plants have evidently undergone much wider changes, until they have finally given rise to new generic types. We are thus forced to conclude that the indigenous endemic genera constitute the most rapidly evolving members of their flora; and it is significant that they include practically nothing but herbaceous species—surely excellent evidence that the herb changes in type more rapidly than the tree or the shrub.

Further evidence pointing to the same conclusion is presented by a study of the distribution of herbs and of woody plants in the modern scheme of botanical classification, for herbs are found to occur in larger groups than woody plants, their genera containing more species and their families more genera. Monotypes and very small genera and families are very much less common among herbs than among woody plants. These facts are what one might expect on the supposition that herbs are changing faster than the rest of the angiospermous vegetation, for the more rapid production of new forms leads to the building up of larger aggregations, and enables genera or families which have become reduced in size through extinction to repair these ravages quickly.

A study of the structure, distribution, and ancestry of herbaceous angiosperms[1] indicates that they have been evolved in comparatively recent times from a woody ancestry, and have undergone practically their whole course of development since the beginning of the Tertiary. As opposed to this rapid change among herbs, we know from fossil evidence that very many woody genera have existed with very little alteration for a much more extended period than the length of the Tertiary—a convincing demonstration of the slowness with which trees and shrubs undergo evolutionary change. Almost all our woody genera bear evidence, in present

[1] E. W. Sinnott and I. W. Bailey, "The Origin and Dispersal of Herbaceous Angiosperms," *Annals of Botany*, XXVIII (1914), 547–600.

distribution or fossil remains, of a considerable degree of antiquity.

To corroborate this testimony as to the relative rapidity of evolution in herbs and in woody plants, data as to their actual rate of change today would be highly desirable; but this is very difficult to obtain. As far as differences in "variability," using the term in its broadest sense, are concerned, the two growth forms seem nearly equal. In both there are many highly variable types and many of great constancy. In the floras of three representative regions—Eastern North America, Australia, and Ceylon—the proportion of varieties and named forms among the woody species is found to be practically the same as among herbs. Nor is there a radical difference between the two in the extent of cross-pollination by insects, although in temperate regions this is somewhat more common among herbs than among trees and shrubs. The difference in length of generation to which we have called attention is probably the most important factor in determining the rate at which they have evolved.

To whatever cause we may attribute it, however, there seems to be little doubt that during the evolution of the angiosperms the primitive, woody element has been developed very much more slowly than the more recent, herbaceous one; and it is this difference which gives us a hint as to the antiquity of the whole group. We find in the angiosperm flora today (dicotyledons alone considered) over 4,200 genera of trees or shrubs, as opposed to only 2,600 genera of herbs. We may be reasonably sure that practically all of these 2,600 genera of herbs have been developed since the beginning of the Tertiary; and if we assume that herbs are producing new types only twice as fast as trees and shrubs—surely a conservative estimate—we must believe that only about 1,300 woody genera have been evolved during the same time. The evolution of the 4,200 genera of woody plants at present existing, to say nothing of the great numbers which have been lost through extinction (by which trees and shrubs have suffered much more than herbs), would therefore require a period at least thrice the length of the Tertiary. If the common assumption that the Tertiary was approximately as long as the Cretaceous is correct,

the origin of the angiosperms would thus be thrust back to a date much earlier than the beginning of the Cretaceous.

Of course such an estimate is hypothetical in the extreme; but by indicating that the history of the woody members of the group extends back over a period many times as long as that during which herbs have existed, it serves to give us a clue as to angiosperm antiquity, and it emphasizes the fact that our present huge array of trees and shrubs, types very slow in changing, must have required an enormous length of time for their evolution. There is evidence, moreover, that evolution took place even more slowly in former times than it does at present, since flower-loving insects, to the agency of which many attribute the rapid development of the angiosperms, did not appear on the scene, at least in numbers, till the dawn of the Tertiary.[1] All this makes it highly probable that these now dominant seed plants did not begin their existence in the early Cretaceous, where they first appear as fossils, but that they had already undergone a long course of evolution before that time. Indeed, the external features, and more particularly the internal anatomy, of these earliest fossil angiosperms are not at all those of primitive types, but exhibit a considerable degree of specialization.[2] To regard such plants as having sprung suddenly into being from gymnospermous ancestors is to overtax the imagination of even an ultra-mutationist.

As to why the earliest members of the group apparently failed to be preserved we cannot be sure, but evidence is at hand that they were upland forms which would tend less frequently to become fossilized. This predilection of primitive angiosperms for an equable, reasonably cool climate, if it can be proved, will lead us to look back to the era of low temperatures in the Jurassic, or perhaps even to as remote a period as the cataclysmic refrigeration of the Permian, for the date when the first angiospermous stock began to be differentiated from its gymnospermous ancestry.

The botanical evidence is therefore overwhelmingly in favor of the conclusion that angiosperms existed for a considerable period

[1] Handlirsch, *Die fossile Insecten.*

[2] M. C. Stopes, "Petrifactions of the Earliest European Angiosperms," *Phil. Trans. Royal Society*, B, 203, pp. 75–100.

previous to the Cretaceous, although this cannot be said to be absolutely proved till they are brought to light as fossils from the earlier periods of the Mesozoic, a discovery which diligent search may reasonably be expected to yield. The establishment for the angiosperms of an antiquity greater than that usually accorded them at the present time will be of some importance geologically, since the occurrence of fossil members of the group in a given formation will no longer be regarded as a demonstration of the post-Jurassic age of the latter.